Mite community composition across a European transect and its relationships to variation in other components of soil biodiversity

Dirilgen, T; Arroyo, J; Dimmer, WJ; Faber, J; Stone, D; Martins da Silva, P; Carvalho, F; Schmelz, R; Griffiths, BS; Francisco, R; Creamer, RE; Sousa, JP; Bolger, T

Published in:
Applied Soil Ecology

DOI:
10.1016/j.apsoil.2015.06.008

First published: 01/01/2016

Document Version
Peer reviewed version

Elsevier Editorial System(tm) for Applied Soil Ecology
Manuscript Draft

Manuscript Number: APSOIL-D-15-00159R2

Title: Mite community composition across a European transect and its relationships to variation in other components of soil biodiversity.

Article Type: SI: Soil Biodiversity

Section/Category: Invertebrate-related Submissions

Keywords: mites, soil biodiversity assessment, cross-taxon congruence

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Abstract: The sustainable use of soils requires the protection of soil biodiversity because of its importance in the delivery of ecosystems services. However, no effective indicator exists which would allow assessment of the current state of biodiversity and is sensitive to change. This study, which is a component of the EcoFINDERS project, examines the use of mites (Acari) as a possible biological indicator of soil community composition. Thirty-six sites were sampled across 10 European countries spanning four bio-climatic zones (Alpine, Atlantic, Continental and Mediterranean) and 3 land uses (arable, grassland and forestry) for both biotic and abiotic variables. Results show a significant effect of bio-climatic zone on mite communities; in particular, the Mediterranean region had a rather distinct composition. Land use type significantly affected mite community composition and there was a distinct association with forestry. Cross-taxon congruence among soil taxa was variable and generally weak. Procrustes analysis showed that there was little similarity between the patterns of variation in mite community composition and those of other taxonomic groups (Collembola, Enchytraeidae, Nematoda and microbes). Mite and Collembola communities had the strongest correlation ($r=0.4316$, $p<0.001$). There was also variation in the indicator values of individual mite groups. Mesostigmata were correlated with soil microbial activity, as assessed using Multiple Substrate Induced Respiration, and Prostigmata with Collembola.

Highlights

Used extensive transect on which multiple aspects of soil biodiversity were measured.

Composition of mite community varied with bio-climatic zone, land-use type.

Mite community primarily related to extent of fungal dominance of microbial biomass.

Composition of Mesostigmata community correlated with microbial activity (MSIR).

At this spatial scale mites do not appear to be a good indicator of overall soil biodiversity.

Mite community composition across a European transect and its relationships to variation in other components of soil biodiversity.

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Abstract

The sustainable use of soils requires the protection of soil biodiversity because of its importance in the delivery of ecosystems services. However, no effective indicator exists which would allow assessment of the current state of biodiversity and is sensitive to change. This study, which is a component of the EcoFINDERS project, examines the use of mites (Acari) as a possible biological indicator of soil community composition. Thirty-six sites were sampled across 10 European countries spanning four bio-climatic zones (Alpine, Atlantic, Continental and Mediterranean) and 3 land uses (arable, grassland and forestry) for both biotic and abiotic variables. Results show a significant effect of bio-climatic zone on mite communities; in particular, the Mediterranean region had a rather distinct composition. Land use type significantly affected mite community composition and there was a distinct association with forestry. Cross-taxon congruence among soil taxa was variable and generally weak. Procrustes analysis showed that there was little similarity between the patterns of variation in mite community composition and those of other taxonomic groups (Collembola, Enchytraeidae, Nematoda and microbes). Mite and Collembola communities had the strongest correlation (r=0.4316, $p<0.001$). There was also variation in the indicator values of individual mite groups. Mesostigmata were correlated with soil microbial activity, as assessed using Multiple Substrate Induced Respiration, and Prostigmata with Collembola.

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1. Introduction

The sustainable use of soils in a world where, at the current rate of human impact, demand for their services will inevitably outweigh the supply, is of major concern. Given the importance of soil biodiversity in maintaining the provision of ecosystem services (Decaëns et al., 2006; Mulder et al., 2011) and the fact that human activities are amongst the main current threats to this biodiversity through soil degradation, land use management, climate change, chemical pollution and invasive species (Lavelle et al., 1997; Bohlen et al., 2004; Decaëns et al., 2006; Feld et al., 2009; Gardi et al., 2009; Straube et al., 2009; Bran Nogueira Cardoso et al., 2013) there has been an increased awareness of the need to protect soil biodiversity.

In order to set a baseline and to monitor changes in this biodiversity there is a need to have accurate indicators of the current state of soil biodiversity (Turbé et al., 2010) and to assess the main trends over time rather than simply have a snapshot of its current state (Noss, 1990). Such indicators should present complex information in a simple and clear manner (Parisi et al., 2005; Turbé et al., 2010) thus enhancing communication and transparency. The criteria for a good indicator will vary depending on the purpose it hopes to serve. The selection of such indicators and the development of an appropriate monitoring scheme are challenging with the present state of our knowledge as the relationship between biodiversity, ecosystem services and function has yet to be fully disentangled. To date, there has been no single method or indicator which reflects all the different aspects of soil complexity (Turbé et al., 2010).

There is a long history of chemical, physical or biological indicators being used in soil science to indicate various aspects of soil health, responses to inputs and management (Bongers,

1990; Schoenholtz et al., 2000; Gulvik, 2007Bastida et al., 2008; Bran Nogueira Cardoso et al., 2013). However, while there may have been an implicit assumption that some of these indicated broader changes in the composition of the soil biota there is still not a universally accepted indicator of soil community assemblage *per se*. Soil biodiversity encompasses a broad range of organisms ranging in size from micrometre to centimetre scale. Microorganisms such as bacteria, fungi, protozoa and algae are thought to be responsible for 60-80% of biological activity within the soil (Petersen and Luxton, 1982). Microfauna such as nematodes, mesofauna such as mites, Collembola, Enchytraeidae and other arthropods are considered to be important for microbial population regulation and nutrient cycling. Lastly, macrofauna including earthworms, isopods, centipedes, millipedes, larger enchytraeids, insects at varying developmental stages, fragment and mix soil components and nutrients and affect overall soil structure (Petersen and Luxton, 1982; Edwards & Bohlen, 1996; McInerney and Bolger, 2000; Sheehan et al., 2006).

Many invertebrate taxa such as Nematoda, Enchytraeidae, and Collembola have been proposed as and are being used as indicators (Bongers, 1990; Parisi et al., 2005) and increasingly, attempts are being made to monitor soil biodiversity and/or its loss. Projects such as the Environmental Assessment of Soil for Monitoring (ENVASSO) attempted to identify indicators for monitoring biodiversity loss for example, and the Ecological Function and Biodiversity Indicators in European Soils (EcoFINDERS) project, of which this study is part, aims to identify bioindicators reflective of biodiversity and ecosystem function at a European scale.

In order to narrow down the wide diversity of soil biota to a list of potential indicators of soil biodiversity a logical-sieve method (Ritz et al., 2009) was used (see Faber et al., 2013 for

86 summary). Despite the ‘taxonomic dilemma of mites’ (Gulvik, 2007), Acarina (i.e. mites)
87 were amongst those shortlisted for investigation.

88 Mites (Arachnida, Acari) are a large and functionally important part of the soil mesofauna
89 (Gulvik, 2007). They are one of the most species rich arthropod taxa. Approximately 45,000
90 species have been described to date, but current estimates of the number of extant species
91 range from 500,000 to a million and they are perceived by many to be a hyperdiverse (or
92 "megadiverse") group (Hammond, 1992; Walter and Behan-Pelletier, 1999; Ødegaard,
93 2000). Mites contribute directly and/or indirectly to the provision of ecosystem goods and
94 services through their intricate relationship with their surrounding biotic and abiotic
95 environment (Lavelle et al., 2006) and in particular through their dietary interactions with
96 the microflora and their predatory interactions with other components of the soil fauna
97 (Laakso et al., 2000).

98 It has been suggested that soil mite communities hold good promise as bioindicators of soil
99 biodiversity because of their stability of community composition, interaction with ecological
100 niches (van Straalen, 1998) as well as their high abundance, diversity and wide spread
101 distribution (Gulvik, 2007). For example, they have been proposed as indicators for
102 assessing soil quality (Behan-Pelletier, 1999; Parisi et al., 2005) and have been used in some
103 monitoring programmes in conjunction with other indicator taxa (such as; BISQ ‘Biological
104 Indicator System for Soil Quality’ in the Netherlands, BBSK ‘Biological Soil Classification
105 Scheme’ in Germany and BSQ ‘Biological Soil Quality’ in Italy).

106 This study explores the hypothesis that mite community composition is correlated with
107 those of other taxonomic groups within the soil. To do this, data on mites, microbes,
108 Collembola, Enchytraeidae, Nematoda, and environmental parameters from thirty-six sites

spanning four bio-climatic zones (Mediterranean, Continental, Atlantic, Alpine) across ten European countries were analysed.

The study assessed the value of mite community composition as an indicator of changes in the structure of other components of the soil biota. This was achieved by assessing the turnover in mite communities over large spatial scales and testing whether such changes reflected those of other components of soil biodiversity. Changes in several sub-groups of mites, often separated in studies of soil fauna (Oribatida, Mesostigmata, Astigmata or Prostigmata), were also examined independently and the effect of taxonomic resolution of mite identification on these relationships was assessed.

2. Methods

2.1 Sampling

A total of 36 sites, representing a subset of the sites described in Stone et al. (2015, this issue) were sampled in spring 2013 across 10 EU countries. These sites encompassed four bio-climatic zones (Mediterranean, Continental, Atlantic and Alpine) and three land use types (grassland, arable and forestry) (Fig. 1). Detailed descriptions of site selection, the sampling strategy and list of the abiotic and biotic variables measured at each site are provided in Stone et al. (2015, this issue). A suite of 22 abiotic measurements (Table 1) were taken at each site in autumn 2012 and pH and SOC (Soil Organic Carbon) were re-sampled in Spring 2013 to check consistency and were found to be the same. A standardised protocol was used to sample various elements of the soil fauna and microflora.

Each site was sampled in autumn 2012 for microbial populations, Enchytraeidae and Nematoda following the methods described in Creamer et al. (2015a, this issue). The data for most of the components of biodiversity are derived from that sampling. An additional sampling for microarthropods was carried out in spring 2013. This was necessary because the microarthropod extraction for the 2012 sampling was unsuccessful. Within each site microarthropods (including mites) were sampled using three 5cm diameter plastic cores to a depth of 5cm. These cores were driven into the soil using a rubber mallet and dug out using a spade in a manner which minimised the compaction of the soil in the core (Stone et al. 2015, this issue). The samples were transferred by courier mail to the laboratory of the partner institute responsible for microarthropod extraction (IMAR, University of Coimbra, Portugal). Upon arrival samples were stored at 20°C for a couple of days until they were placed in a High-Gradient Macfadyen extractor for 7 days to extract soil microarthropods. After extraction and sorting, mites were stored in 80% ethanol and sent to laboratories at either; University College Dublin, Ireland, or Alterra, The Netherlands, for identification.

Mites, Collembola (Martins da Silva et al. 2015, this issue) and Enchytraeidae were identified to species level, the nematodes to functional group (Stone et al. 2015, this issue) and microbial populations were measured using phospholipid-derived fatty acids (PLFA) (Francisco et al., 2015, this issue) and Multiple Substrate Induced Respiration via MicroRespTM (MSIR) (Creamer et al., 2015b, this issue). All mites were slide-mounted in Hoyers medium (Krantz 1978) and identified to species level where possible using the keys of Weigmann (2006), Balogh & Balogh (1992), for oribatids; Karg (1993, 1989), Evans (1977), Evans & Till (1979) and Bhattachharyya (1963) for mesostigmatids; Dindal (1990) for astigmatids; Sig Thor (1933), Gilyarov (1978) and Mahunka (1965) for prostigmatids.

153 ***2.2 Statistical analysis***

154 The average abundance in the three samples from each site was used throughout the
155 analyses. Mite data were log (Y + 1) transformed prior to analysis.

156 Constrained Canonical Correspondence Analysis (CCA) was used to assess the relationships
157 between environmental variables (explanatory variables) and mite community composition
158 (response variable). Bio-climatic zone and land use type were introduced as factors while
159 microbial and environmental parameters were considered to be continuous variables. In the
160 analysis of the abiotic parameters a stepwise variable selection was used based on the
161 Akaike Information Criterion (AIC) to select the five most significant variables and which
162 contributed most to describing the inertia in community composition. At each step, only
163 variables explaining a significant ($P < 0.05$, Monte Carlo test with 999 permutations)
164 proportion of the remaining variation were included.

165 Procrustes analysis was used to investigate the degree of concordance among the variation
166 in mite and the other biotic data sets thus providing an indication of the value of mite
167 community data in predicting biodiversity of community composition of other soil taxa. The
168 first four ordination axes were used as input. These were derived from Detrended
169 Correspondence Analysis (DCA) for mites (species, family and sub-groups), Collembola,
170 Enchytraeidae and from Principle Components Analysis (PCA) for the nematode functional
171 groups and the microbial assessments of community structure. The mite, nematode and
172 enchytraeid data were log transformed and the PLFA was transformed using log(1000y+1)
173 transformation. CCA, DCA and PCA analyses were carried out using Canoco for Windows
174 (version 5) (ter Braak and Šmilauer 2012) and Procrustes analysis was performed using the

175 Protest function in the 'Vegan' package (Oksanen et al., 2012) of the R software v.2.15.0
176 (2012) (R Development Core Team, 2012).

177

178 **3. Results**

179 ***3.1 Variation between Bio-climatic Zones and between Land Use Types***

180 One hundred and eighty six mite taxa were recovered from the 36 sites (Appendix 1). There
181 were 101 Oribatida, 56 Mesostigmata, 26 Prosigmata and 3 Astigmata taxa with an overall
182 β-diversity of 7.3 S.D. units as represented by species turnover in Detrended
183 Correspondence Analysis (DCA). The composition of the mite community varied
184 significantly amongst the bio-climatic zones and land uses. The fauna of the Mediterranean
185 region was most distinct with many Prostigmata and Oribatida taxa occurring most
186 frequently in those sites (F=1.4, p= 0.002) (Fig. 2) and abundances of over 30 X 10^3 m^{-2}. A
187 similar pattern was seen when only Oribatida were included in the analysis (F=1.6, p=004).
188 Several species such as *Adelphacarus sellnicki*, *Allogalumna alamellae* and *Passalozetes*
189 *africanus* appear to be highly associated with the Mediterranean, while *Ceratozetes*
190 *laticuspidatus, Lucoppia burrowsi* and *Malaconothrus monodactylus* are amongst those
191 associated with the Alpine region and *Dissorhina ornata* and *Phthiracarus compressus*
192 occurred most frequently in the Atlantic Region (Fig. 3a). Although the vast majority of the
193 Mesostigmata did not occur as frequently in the Mediterranean region the effect of bio-
194 climatic zone was not significant (F=1.2, p=0.064) (Fig. 3b). However, one species,
195 *Dendroseius reticulatus*, did occur exclusively in one of the Mediterranean sites.

196 The fauna also varied significantly between land use types (F = 1.3, P= 0.002) (Fig. 4) with
197 average abundances in the arable sites of 4.2 X 10^3 m^{-2} and of 26 X 10^3 m^{-2} in the forest sites.
198 The first and second axes of the ordination show that the communities occurring in forestry
199 were most distinct from those occurring in arable and grassland sites. A large number of
200 oribatid species occurred most regularly in forestry (Fig 5a) while the preferences of the
201 mesostigmatid taxa were more evenly spread across all three land use types (Fig 5b).

202 ***3.2 Relationships between mites and microbial populations***

203 The relationship between mites and microflora was analysed by using the microbial
204 parameters as "environmental variables", these included molecular microbial biomass and
205 summary data from PLFA. This analysis indicated that the oribatid fauna were particularly
206 influenced by fungal to bacterial ratio (F:B) and 16:1 ω5c, which is an indicator of the
207 abundance of Arbuscular Mycorrhizal Fungi (p=0.004), which accounted for 27.93% of the
208 inertia in mite species abundance (Fig. 6a). The other microbial parameters associated with
209 the second axis accounted for a further 22% of the inertia. These microbial parameters are,
210 however, also associated with land use type and therefore it is not clear whether it is land
211 use, or the microbial populations *per se*, which are the drivers of the mite community
212 composition.

213 Mesostigmata, which are predominantly predatory, were not significantly associated with
214 fungal communities (F=1.2, p=0.084). However, the majority of the species occurred in sites
215 with lower microbial biomass while *Prozercon* sp., *Lysigamasus vagabundus* and *Veigaia*
216 *cerva* do appear to be associated with increased microbial biomass and an increased
217 predominance of fungi but these are also the species which were identified as favouring

forest habitats. There are some species such as *Dinychus* sp., *Arctoseius cetratus* and *Lysigamasus parrunciger*, which appear not to be related to microbial biomass (Fig 6b).

3.3 Effects of abiotic variables

Twenty two abiotic variables were measured at each site (Table 1) and the relationship between these and mite community composition was assessed by the forward selection of the variables in CCA (Fig. 7). The factors which explained most of the variation in mite community composition were base saturation (Bsa) (4.5%), exchangeable K (KE) (4.4%), Moisture content of non-sieved sample (MC1) (4.1%), soil Nitrogen content determined by combustion (N) (4.1%) and soil texture as expressed by loamy soils (3.9%). These suggest that pH, bulk density/porosity, water content and quantity and quality of organic matter are critical in determining the mite community structures but it is not clear how exchangeable K might affect the animals.

3.4 Congruence between variations in mite community composition and those of other soil taxa

Procrustes analysis shows that there was little similarity between the patterns of variation in mite community composition and those of other taxonomic groups. At the species level there was a significant correlation with Collembola ($r=0.4316$, $p<.001$) (Table 2). The weakest relationship was between mites and Enchytraeidae ($r= 0.2436$) and neither of the microbial community measures (MSIR and PLFA) or the nematode functional group composition were significantly associated with mites (Table 2).

The level of taxonomic resolution used for the mite classification (species versus family versus sub- group level identification) had an effect on the levels of congruence (Table 2).

240 The significant relationship with collembolan community composition was lost at family
241 level but at sub-group resolution there was a significant correlation with Collembola,
242 Enchytraeidae and Multiple Substrate Induced Respiration (MSIR).

243 Investigation into whether the use of a single sub-group of mites (Oribatida, Mesostigmata,
244 Astigmata or Prostigmata) would indicate the same congruence as studying mite community
245 as a whole was quite variable (Table 2). The variation in Mesostigmata was correlated with
246 MSIR and Prostigmata were correlated with Collembola.

247

248 **4. Discussion**

249 The data from these transects show that mites are responsive to large scale environmental
250 conditions and that there is a significant turnover in mite community composition between
251 different bio-climatic zones and between land use types. These changes appear to reflect
252 changes in the availability of food sources, such as fungi and soil organic materials, and the
253 physical nature of the soils, such as pH, porosity and water availability. However, in a large
254 scale survey such as this one, they do not appear to respond to environmental variation in
255 the same way as many other taxa which occur in the soil.

256 While mite community composition was not related to the latitude of the sampling sites
257 (results not shown), there were significant differences amongst bio-climatic zones. The
258 Mediterranean fauna were particularly distinct and separated on the first axis of all the
259 ordinations. The separation of this fauna from the others is most likely related to the
260 moisture conditions of these soils which would be exposed to prolonged periods of dryness
261 in the summer months.

While many mite species have relatively cosmopolitan distributions there is also significant turnover in species composition between major bio-climatic zones. For example, approximately 50% of the oribatid mites that occur in Europe are confined to this region (Schatz 2004). Similarly, within North America, Behan-Pelletier and Schatz (2010) found a turnover of approximately 50% of the species of Ceratozetoidea between one region and another. Amongst the Mesostigmata the rate of endemism in the major global biogeographic zones is approximately 60% for the Phytoseiidae (Tixier et al., 2008) all of which suggest that such a turnover between bio-climatic zones is to be expected. Indeed, Erdmann et al. (2012) have emphasised the importance of regional differences in determining the mite fauna of forests.

Mite communities are known to be influenced by land use and management practices (Behan-Pelletier, 1999) and this was also seen in this study. The preferential occurrence of oribatids in forestry is to be expected as oribatids are a dominant component of the microarthropods in most forest soils (Petersen and Luxton, 1982). The observed difference between the two groups is likely to be reflective of the feeding strategies. Mesostigmata are pre-dominantly predatory; (many Uropodina are nematode feeders (Klarner et al. 2013) but some are omnivores and also feed on detritus and fungi (Gulvik, 2007)) compared to Oribatida which, although they contain a broad range of feeding types (Schneider et al., 2004) are mainly fungal and bacterial feeders (Laakso et al., 2000, Maraun et al., 2011).

The use of any single taxon as an indicator of biodiversity assumes that there is cross-taxon congruence in the patterns of variation between different taxa. Such congruence can arise because there is (i) similar responses of different taxonomic groups to the same environmental gradient(s), (ii) responses to different but correlated environmental

gradients, (iii) biotic interactions (iv) a random draw of species from regional species pool, and (v) inconsistent sampling effort (where some sites may be sampled more efficiently for multiple taxa) (Gaston, 1996). The variation in the composition of the mite and Collembola communities was correlated which would imply that these taxa either respond to environmental factors in a similar manner or respond to correlated environmental parameters (Table 2). Despite the fact that mites and Collembola may have differing life-history strategies, both groups are arthropods which live within the soil pore space, use organic matter and microbial tissue as sources of food or feed on each other, and respond in similar fashions to factors such as soil moisture content. Therefore it is not unexpected that their community compositions would be correlated.

At low levels of taxonomic resolution there is a significant relationship between mites and some properties of the microfloral community (Fig. 6, Table 2). This is presumably related to the biotic interactions between these groups, as many of the mites are microbivores. However, the fact that this is seen only at low levels of taxonomic resolution may reflect a prevalence of non-selective feeding and significant dietary niche overlap amongst the mites. There is also considerable evidence for some degree of dietary specialisation (Shaw, 1988; Walsh and Bolger, 1990; Maraun et al., 2011;) which would appear to contradict this idea; however, it is also known that soil food webs are characterised by the presence of many omnivorous species (Digel et al., 2014). The significant relationship between Mesostigmata and MSIR may be a reflection of a trophic cascade as the presence of Mesostigmata affects the abundance of microbivores which would in turn affect the microbial biomass (Hendrix et al., 1986).

307 The relationship with Enchytraeids is perhaps also to be expected as enchytraeid
308 distribution is largely determined by soil water content, pH and organic matter content
309 (Didden, 1993) all of which also affect the abundance of mites. The fact that the relationship
310 was only seen at sub-group level again suggests that the relationship exists because of
311 related effects of environmental conditions rather than interspecific interactions.

312 Although several comparisons showed significant correlations it should be noted that
313 randomization tests can lead to elevated levels of significance and that therefore the value
314 of the correlations should also be taken into account (Heino, 2010). In this study, the highest
315 correlation achieved was 0.4316 which would indicate disagreement value of greater that
316 80%. Thus even where there is significant correlation, the value of any single taxon in
317 predicting the response of another is very weak.

318 It is obvious from this study that it is highly unlikely that a single taxon indicator of soil
319 biodiversity is going to be found which is applicable across a large spatial scale. This study
320 was carried out to test whether variations in mite community composition could be used as
321 an indicator of change in other components of soil biodiversity. The results suggest that, at
322 this large scale, limited relationships exist and that therefore they may not be good
323 indicators. This is in contrast to the many studies which suggest that mites are useful
324 indicators. Two aspects of the methods used here may explain this. Firstly, the spatial extent
325 of this study is greater than most studies from the past which concentrated on either single
326 experimental setups or single geographical areas. The larger scale means that altered
327 variations in relationships between taxa in different climatic and bio-climatic zones and land
328 uses are likely to affect potential relationships. This scaling effect can be seen in
329 comparisons of several studies. For example, in the case of oribatid mites, Zaitsev et al.

(2013) have shown that at large spatial scales post-glacial age is important in determining the community composition while at a smaller scale regional factors become important (Erdmann et al., 2012) but at a more local scale relationships with vegetation type and management become important (Bolger et al., 2014). Shevtsov et al. (2013) found that even within a relatively local gradient, the only guild pairs that exhibited higher than expected similarities in species turnover were plants–fungi, fungi–Collembola and Collembola–Mesostigmata all of which are adjacent in the food chain and would be expected to interact directly. Indeed, even within a site that the effect of management can vary between the litter layer and bulk soil and interacts with litter chemistry and climate during decomposition to determine the composition of arthropod communities (Wickings and Grandy, 2013). Secondly, the mites were sampled at a different time to some of the other biota used. This may affect the relationships because the abundance and activity patterns of virtually all components of the soil biota are seasonal (Petersen and Luxton, 1982 *inter alia*). However, on a large scale such as used in this study, such differences would have to be overcome by any method employed. Seasonality and climatic features are always going to vary across the area of the study.

In conclusion, strong correlations between mites and other soil taxa would have facilitated the use of a single taxonomic group for predictive purposes. However, as frequently emphasised in the literature, for better resolution, we still need information on the entire soil biological community (van Straalen, 1998) as well as alpha, beta and gamma diversity (Whittaker, 1960). It therefore appears that with our current knowledge, the search for one bioindicator of soil biological diversity is some way away as no single taxon can be expected

to adequately indicate patterns for all other taxa at the spatial scale examined in this study (Pearson, 1994).

Acknowledgements

This work was supported by the European Commission within the EcoFINDERS project (FP7-264465)

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531 **Tables**

532 **Table 1.** Soil chemical/physical variables measured at each site

533

Moisture Content of non-sieved sample (ml g^{-1})
Moisture Content of 2 mm sieved sample (ml g^{-1})
Average mass of soil in 98 cm^3 core Fresh Weight (g)
WHC (ml 100 g fresh $soil^{-1}$)
Total N by combustion (%)
Total C by combustion (%)
Organic C by combustion (%)
pH
Clay %
Silt %
Sand %
Texture
CEC (cmol +charge kg-1)
Exchangable Ca (cmol kg soil-1)
Exchangable Mg (cmol kg soil-1)
Exchangable Na (cmol kg soil-1)
Exchangable K (cmol kg soil-1)
Base saturation (%)
Average Fresh Weight (g) in core SPRING (g)
Moisture Content of non-sieved sample SPRING (ml g^{-1})
Amount of NO_2-N released (ng/g soil dm/h)
% moisture

534

535

536 **Table 2**. Procrustes analyses of congruence in community composition among mites at varying levels
537 of taxonomic resolution and other taxonomic groups (where 'MSIR', Multiple Substrate Induced
538 Respiration measured using MicroRespTM and 'PLFA', phospholipid-derived fatty acids represent
539 differing microbial population measurement techniques). The values presented are the correlations
540 in a symmetric Procrustes rotation.

541

Component	MSIR	PLFA	Collembola	Enchytraeidae	Nematoda
mite species	0.3434	0.2872	0.4316***	0.2436	0.3475
mite family	0.2532	0.2658	0.2616	0.3325	0.322
mite sub-group	0.3883*	0.2213	0.369*	0.4018**	0.2863
Oribatida	0.3203	0.3136	0.1922	0.2799	0.2855
Mesostigmata	0.3944**	0.211	0.2293	0.2171	0.2743
Prostigmata	0.3127	0.2482	0.3871*	0.3056	0.2593

542

543
*Significant at the 0.05 probability level.
**Significant at the 0.01 probability level. 544
***Significant at the 0.001 probability level.
545

546

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548

549 **Figures**

550 **Fig. 1** Map of Europe showing locations of sites across the different bio-climatic zones

551

552 **Fig. 2** Canonical correspondence analysis (CCA) of log transformed mite taxa across four bio-climatic
553 zones. The first two axes account for 11.7% of the taxa bio-climatic region relationship and the first
554 and trace are significant (F=1.4, p= 0.002). Only the twenty species whose best fit the model are
555 illustrated and labels were adjusted to improve the graph. (Species abbreviations as in Appendix 1)

556

557 **Fig.3** Canonical correspondence analysis (CCA) of mite taxa **(a)** Oribatida and **(b**) Mesostigmata
558 across four bio-climatic zones. The first two axes account for 14.2% and 12.7% respectively of the
559 taxa bio-climatic zone relationship (F= 1.6, p=0.004; F= 1.2, p= 0.064 respectively). Only the thirty
560 species whose best fit the model are illustrated and labels were adjusted to improve the graph.
561 (Species abbreviations as in Appendix 1)

562

563 **Fig. 4** Canonical correspondence analysis (CCA) of mite taxa across land use type. The first two axes
564 account for 7.4% of the species land use relationship and the first axis and trace are significant
565 (F=1.3, p=0.002). Only the thirty species whose best fit the model are illustrated and labels were
566 adjusted to improve the graph. (Species abbreviations as in Appendix 1)

567

568 **Fig. 5** Canonical correspondence analysis (CCA) of mite taxa **(a)** Oribatida and **(b**) Mesostigmata
569 across land use type. The first two axes account for 9.2% and 8.3% respectively of the species land
570 use relationship and the first axis and trace are significant (F=1.5, p=0.002; F=1.2, p=0.034

571 respectively). Only the thirty species whose best fit the model are illustrated and labels were
572 adjusted to improve the graph. (Species abbreviations as in Appendix 1)

573

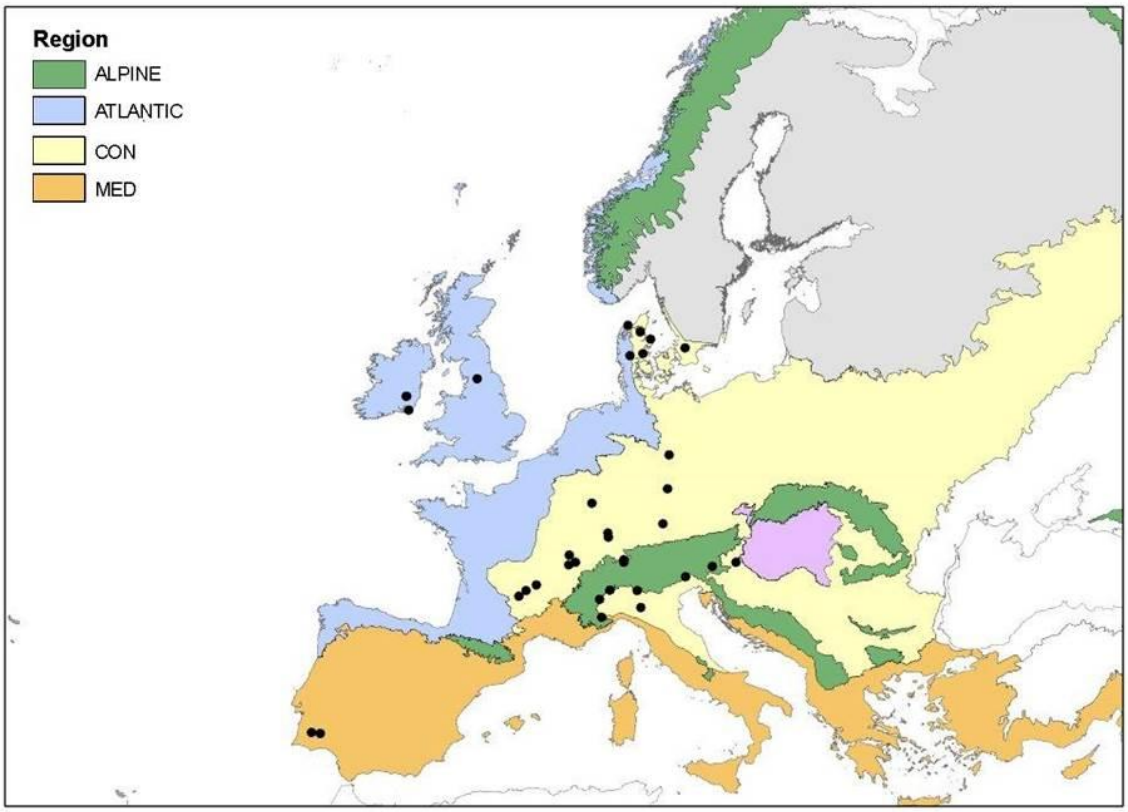
574 **Fig. 6** Canonical correspondence analysis (CCA) of mite taxa **(a)** Oribatida and **(b**) Mesostigmata with
575 microbial parameters. The first two axes account for 22.5% and 20.6% respectively of the mite taxa –
576 microbial relationship (F=1.6, p=0.002; F=1.2, =0.084). Only the fifty and thirty species respectively
577 whose best fit the model are illustrated and labels were adjusted to improve the graph. (Species
578 abbreviations as in Appendix 1)

579

580 **Fig. 7** Canonical correspondence analysis (CCA) of log transformed mite taxa against abiotic
581 characteristics of site. The environmental parameters listed were forward selected and the first five
582 are illustrated. Only the forty species whose best fit the model are illustrated and labels were
583 adjusted to improve the graph. (Species abbreviations as in Appendix 1, Environmental parameters
584 are Bsa -base saturation, KE- exchangeable K, MC1 – Moisture content of non-sieved sample, N – soil
585 Nitrogen content determined by combustion and soil texture as expressed by loamy soils).

586

587 **Figure 1**



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591 **Figure 2**

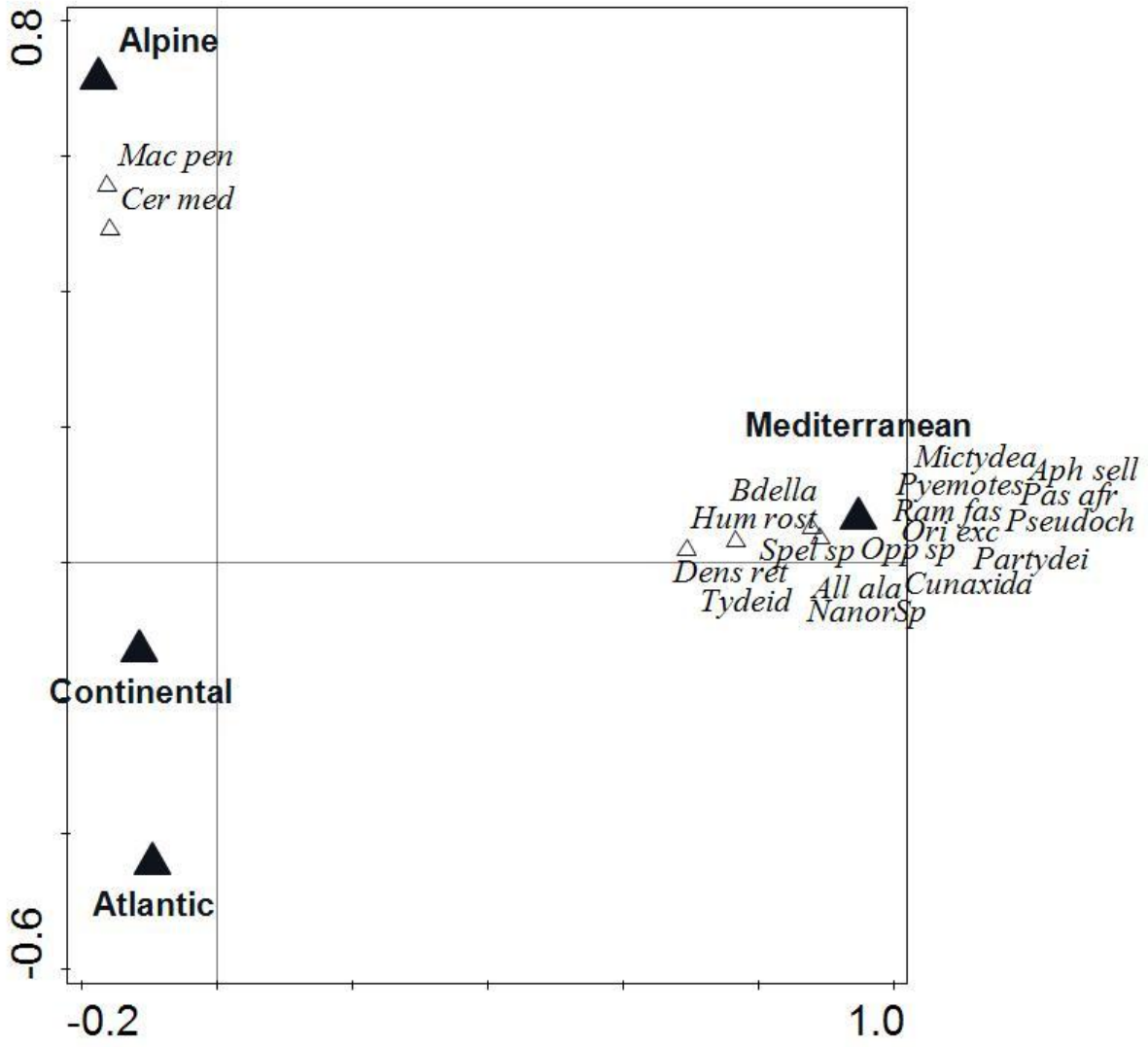

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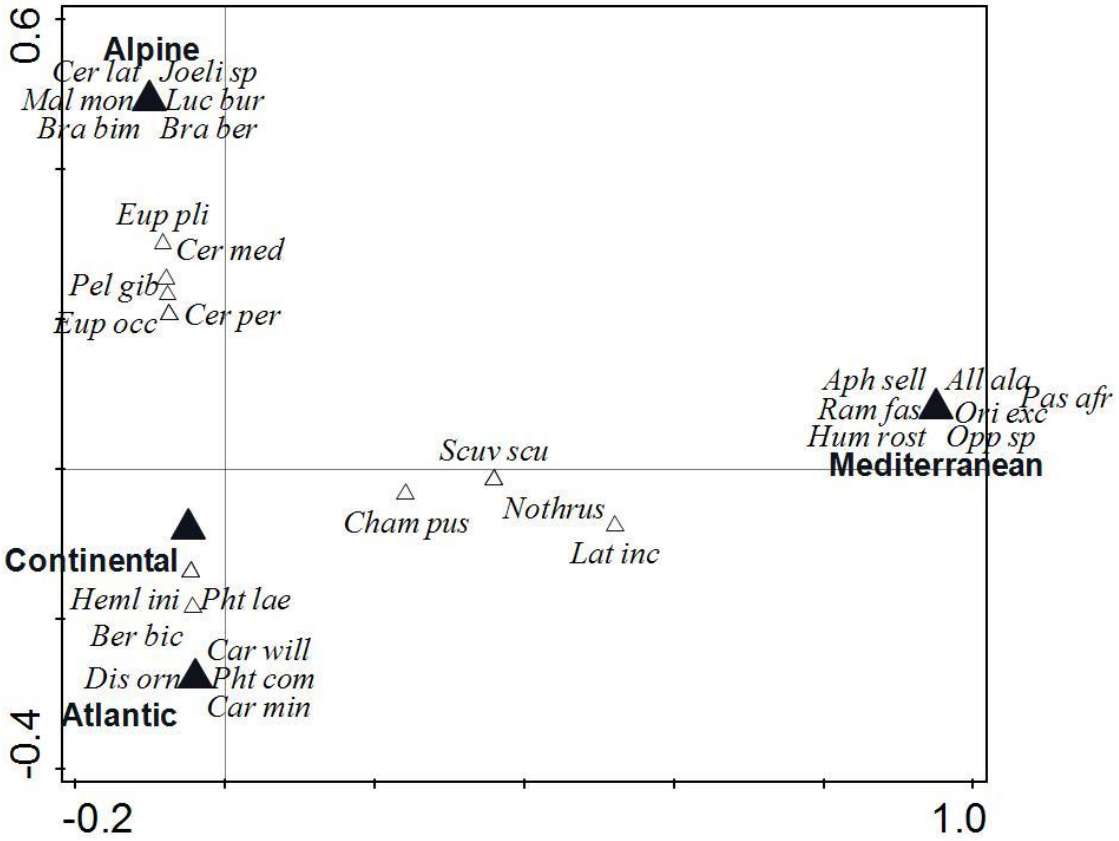
Figure 3a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597 **Figure 3b**

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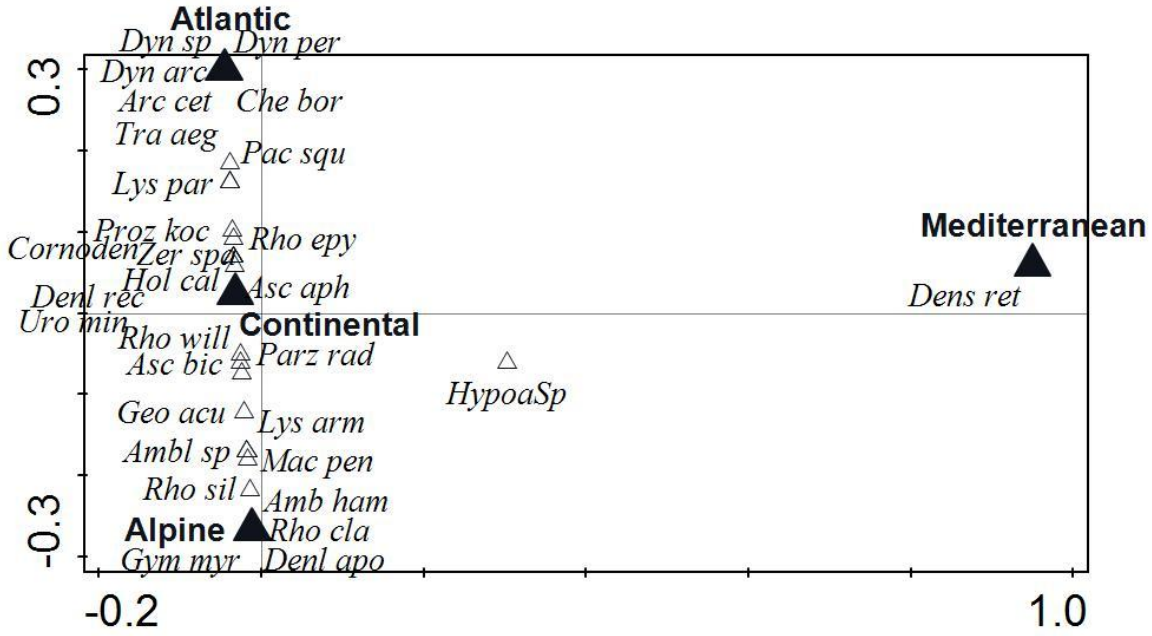

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601 **Figure 4**

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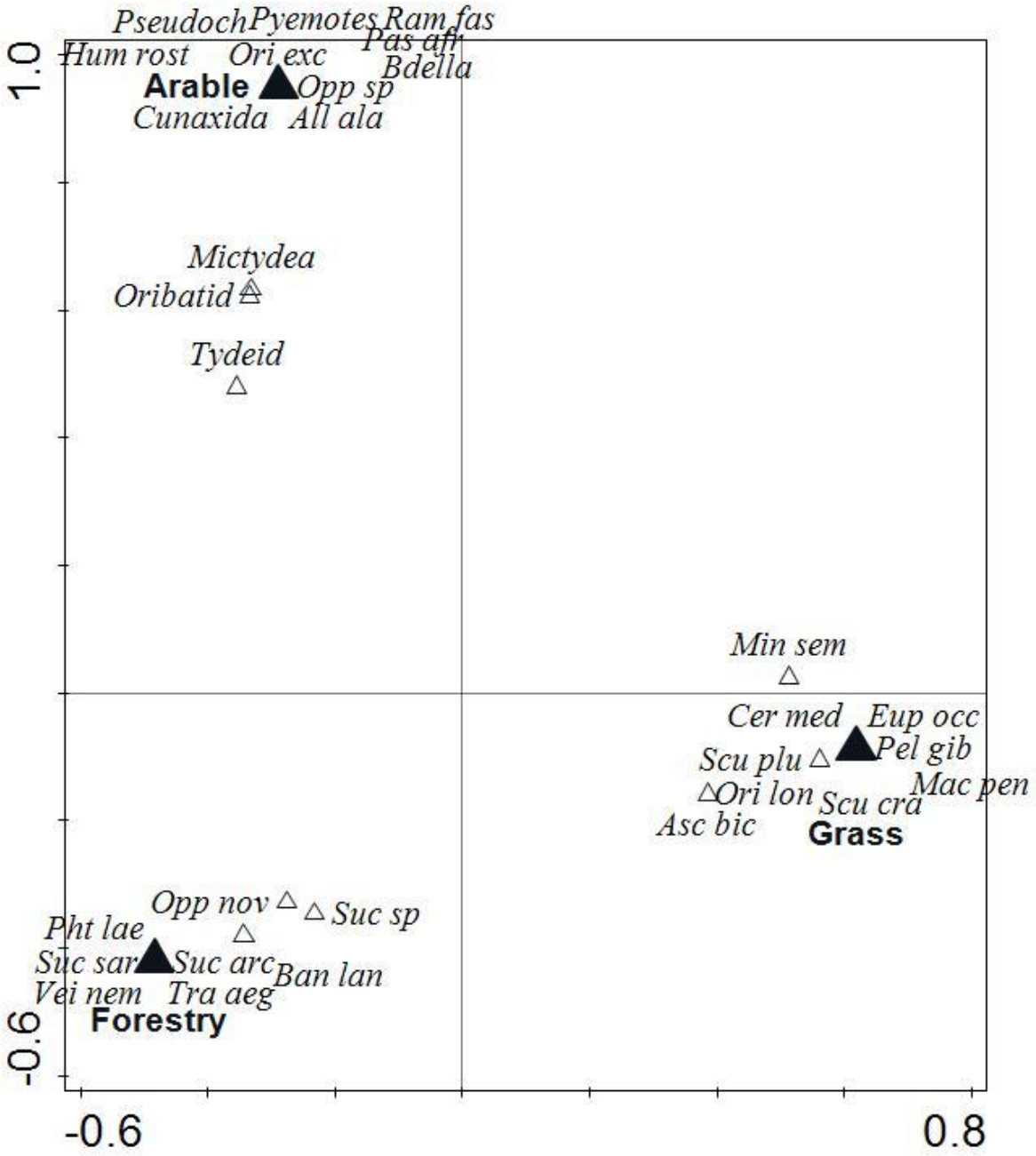

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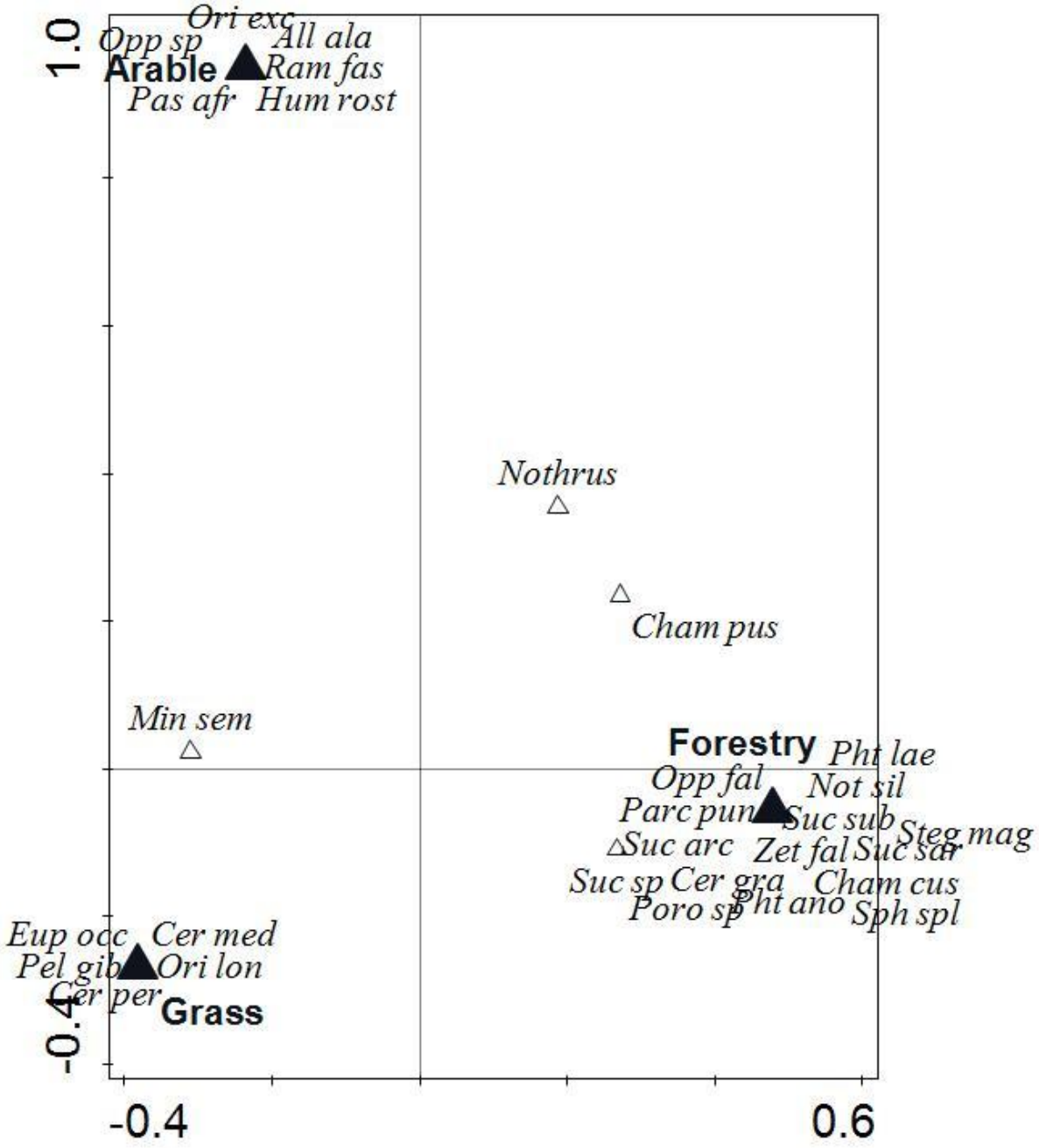
605 **Figure 5a**

606



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609 **Figure 5b**

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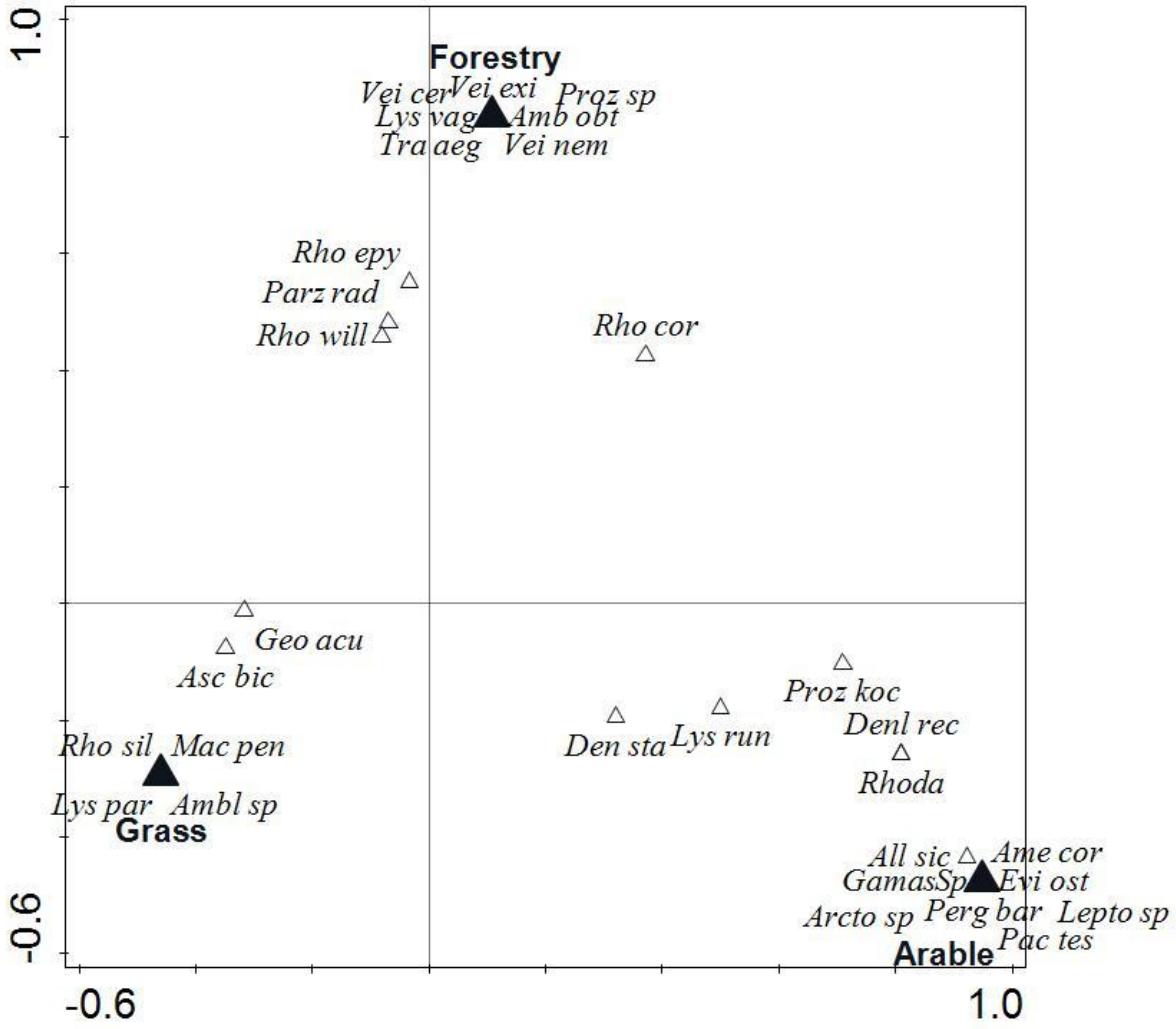

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613 **Figure 6a**

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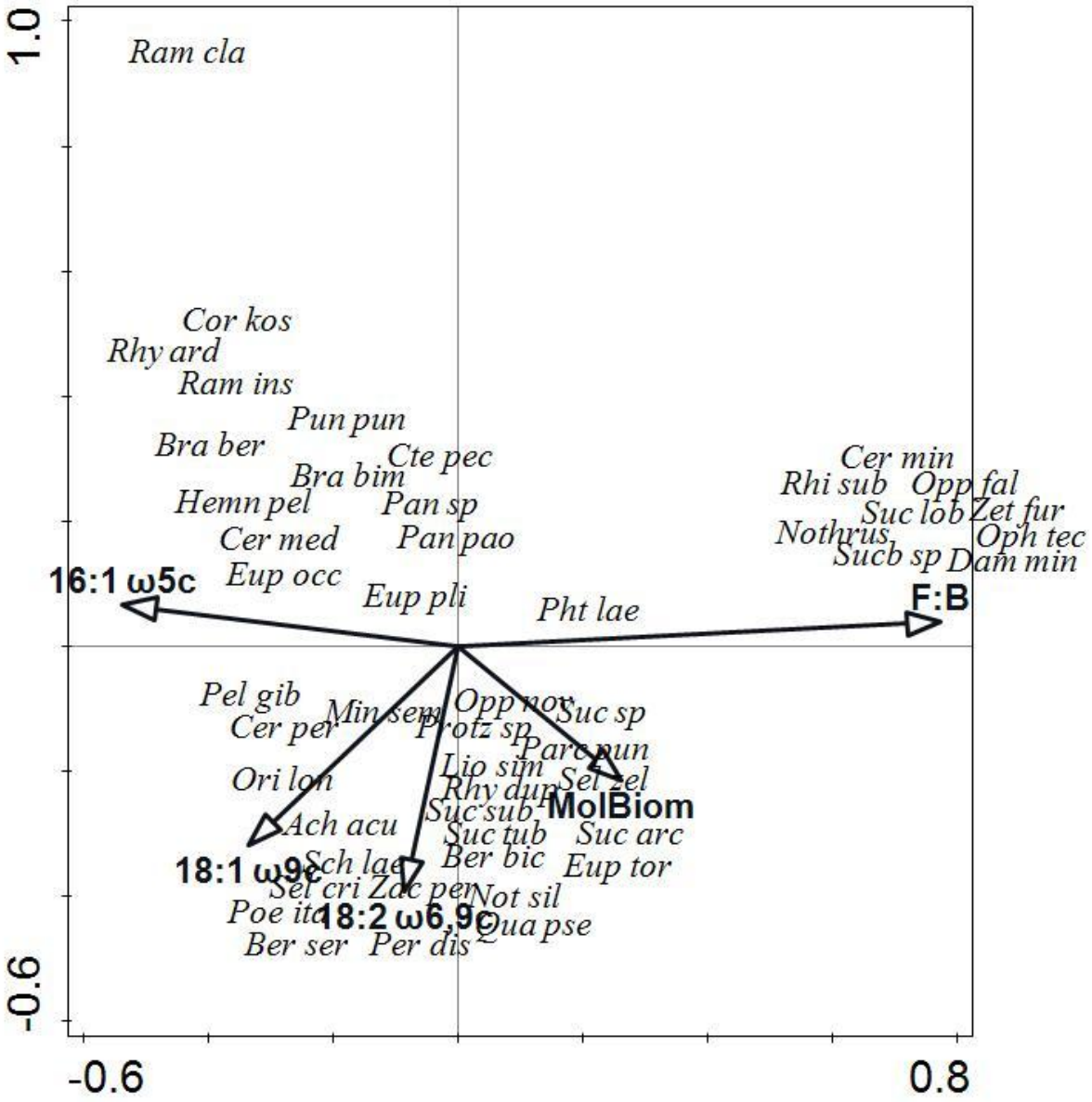

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617 **Figure 6b**

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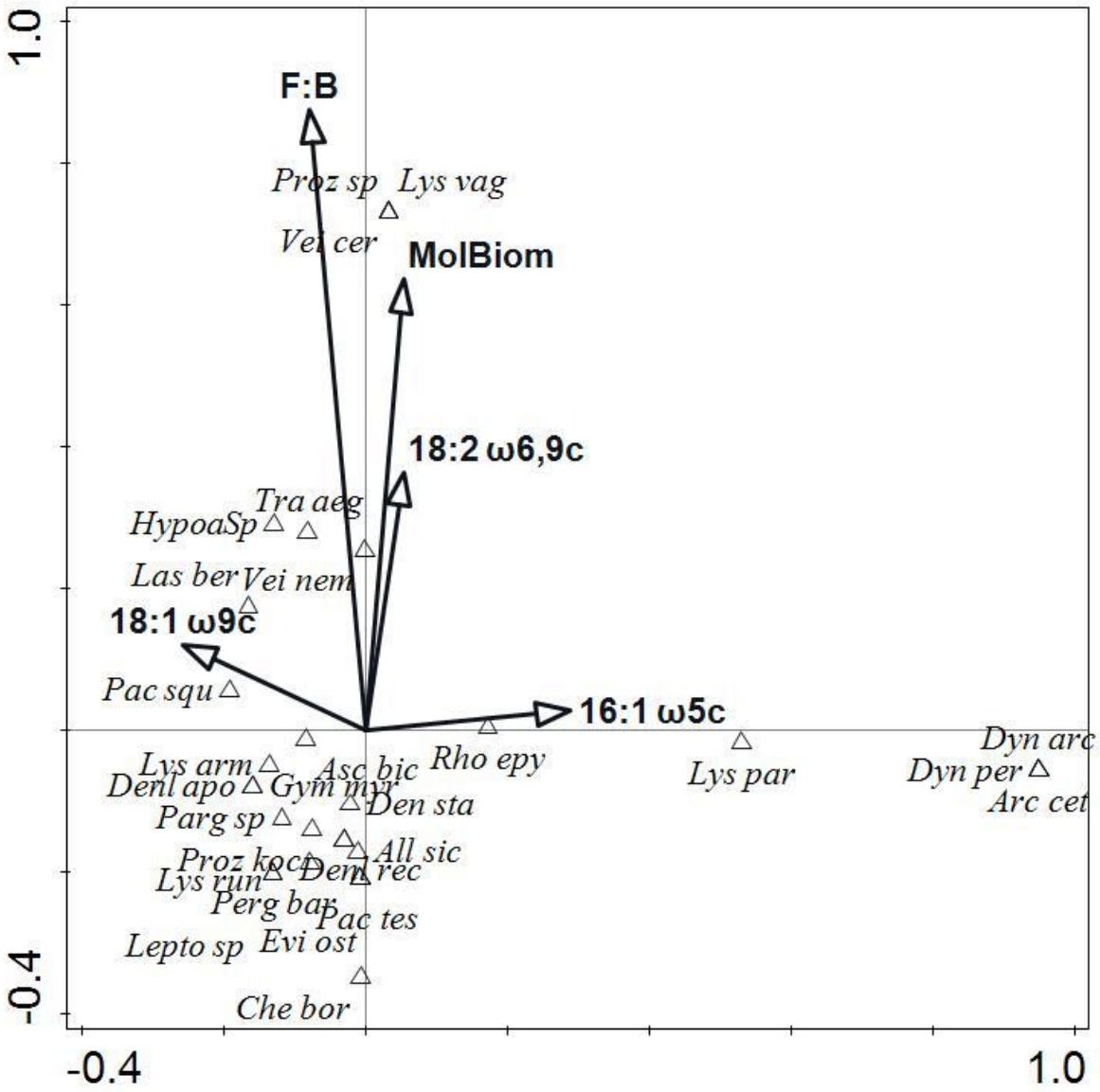

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621 **Figure 7**

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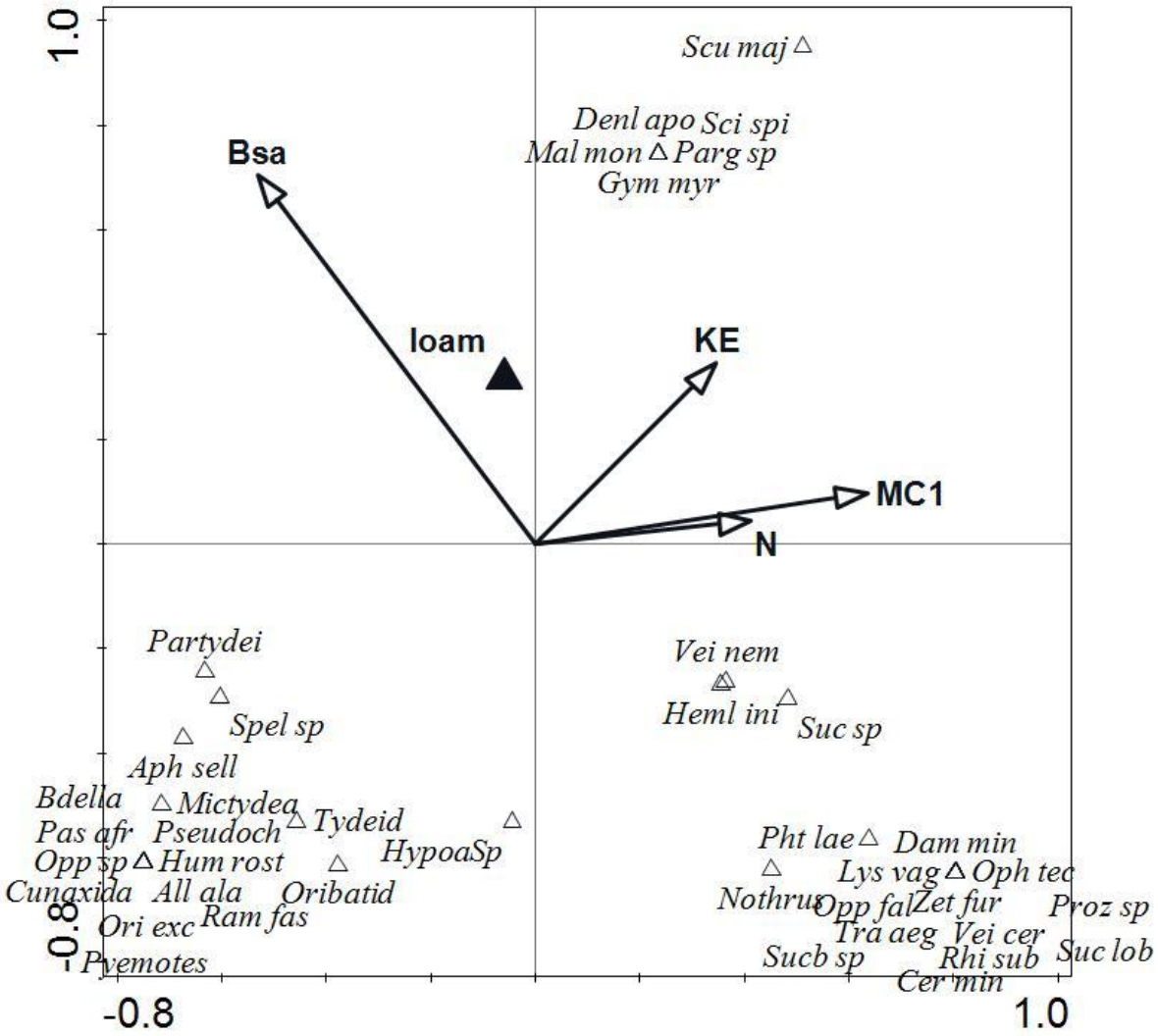

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Appendix 1

Species found in each of the bio-climatic zones and land use types.

Abbreviations; Al: Alpine, Con: Continental, Med: Mediterranean, At: Atlantic, Gr: Grassland, For: Forestry, Ara: Arable

,

Taxon	Abbreviation	Al Gr	Con For	Con Ara	Con Gr	Med For	Med Ara	At For	At Ara	At Gr
Oribatida										
Oribatida	Oribatid		+				+			
Achipteriidae										
Achipteria acuta Berlese, 1908	Ach acu		+		+				+	
Achipteria coleoptrata Linnaeus, 1758	Ach col	+	+		+					+
Parachipteria punctata Nicolet, 1855	Parc pun		+					+		
Brachychthoniidae										
Brachychthonius berlesei Willmann, 1928	Bra ber	+								
Brachychthonius bimaculatus Willmann, 1936	Bra bim	+								
Liochthonius brevis (Michael, 1888)	Lio bre				+			+		
Liochthonius sellnicki (Thor, 1930)	Lio sel				+			+		
Liochthonius simplex (Forsslund, 1942)	Lio sim		+		+					
Poecilochthonius italicus Berlese, 1910	Poe ita				+					
Sellnickochthonius cricoides (Weis-Fogh, 1948)	Sel cri				+					
Sellnickochthonius zelawaiensis (Sellnick, 1928)	Sel zel		+							
Camisiidae										
Heminothrus (P.) peltifer (C. L. Koch, 1839)	Hemn pel		+							+
Carabodidae										
Carabodes minusculus Berlese, 1923 (C.)	Car min							+		
Carabodes willmanni Bernini, 1975 (C.)	Car will							+		
Ceratozetidae										
Ceratozetes gracilis (Michael, 1884)	Cer gra		+							

Ceratozetes laticuspidatus Menke, 1964	Cer lat	+										
Ceratozetes mediocris Berlese, 1908	Cer med	+				+						
Ceratozetes minimus Sellnick, 1928	Cer min		+									
Ceratozetes peritus Grandjean, 1951	Cer per	+				+						
Protozetomimus sp.Pérez- Íñigo, 1990	Protz sp		+			+						
Latilamellobates incisellus (Kramer, 1897)	Lat inc							+				
Trichoribates novus (Sellnick, 1928)	Tri nov		+	+		+				+		
Chamobatidae												
Chamobates cuspidatus (Michael, 1884)	Cham cus		+									
Chamobates pusillus (Berlese, 1895)	Cham pus		+					+				
Ctenacaridae												
Adelphacarus sellnicki Grandjean, 1952	Aph sell						+	+				
Ctenobelbidae												
Ctenobelba pectinigera (Berlese, 1908)	Cte pec					+						
Damaeidae												
Damaeobelba minutissima (Sellnick, 1929)	Dam min		+									
Porobelba sp.Grandjean, 1936	Poro sp		+									
Galumnidae												
Allogalumna alamellae (Jacot, 1935)	All ala							+				
Galumna lanceata Oudemans, 1900	Gal lan		+			+				+		
Hemileiidae												
Hemileius initialis (Berlese, 1908)	Heml ini		+			+				+		+
Humerobatidae												
Humerobates rostrolamellatus Grandjean, 1936	Hum rost							+				
Liebstadiidae												
Liebstadia similis (Michael, 1888) (*Notaspis*)	Lie sim			+		+						
Malaconothridae												
Malaconothrus monodactylus (Michael, 1888)	Mal mon	+										
Nanhermanniidae												

Nanhermannia dorsalis (Banks, 1896)	Nna dor	+						
Nanhermannia nana Nicolet, 1855	Nan nan	+	+					
Nothridae								
Nothrus sp.Koch, 1836	Nothrus		+				+	
Nothrus silvestris Nicolet, 1855	Not sil		+					+
Oppiidae								
Berniniella bicarinata (Paoli, 1908)	Ber bic				+			+
Berniniella nr *serratirostris* (Golosova, 1970) (*Oppia*)	Ber ser				+			
Corynoppia kosarovi Jeleva, 1962	Cor kos	+			+			
Dissorhina ornata (Oudemans, 1900)	Dis orn							+
Lauroppia(Oppiella) falcata (Paoli, 1908)	Opp fal		+					+
Medioppia subpectinata (Oudemans, 1900)	Med sub		+	+	+			
Microppia minus Paoli, 1908	Mic min	+	+	+	+			
Oppiella sp.Jacot, 1937	Opp sp						+	
Oppiella (Rhinoppia) subpectinata (Oudemans, 1900)	Rhi sub		+				+	
Oppiella falcata (Paoli, 1908)	Opp fal		+					
Oppiella nova (Oudemans, 1902)	Opp nov	+	+	+	+			+
Ramusella (I.) elliptica (Berlese, 1908)	Ram ell			+				
Ramusella (I.)insculpta (Paoli, 1908)	Ram ins	+			+			
Ramusella (R.) clavipectinata (Michael, 1885)	Ram cla				+			
Ramusella fasciata (Paoli, 1908)	Ram fas						+	
Oribatellidae								
Joelia sp.Oudemans, 1906	Joeli sp	+						
Ophidiotrichus tectus (Michael, 1884)	Oph tec		+					
Oribatulidae								
Lucoppia burrowsi (Michael, 1890)	Luc bur	+						
Oribatula cognata (Oudemans, 1902)	Ori cog			+	+			
Oribatula connexa Berlese, 1904	Ori con			+	+			
Oribatula[i] *excavata* Berlese, 1916	Ori exc						+	

Oribatula longelamellata Schweizer, 1956	Ori lon	+			+							
Oribatula undulata (Berlese, 1916)	Ori und			+	+							
Oribotritiidae												
Rhysotritia ardua (C. L. Koch, 1841)	Rhy ard	+			+							
Rhysotritia duplicata (Grandjean, 1953)	Rhy dup		+									
Passalozetidae												
Passalozetes africanus (Grandjean, 1939)	Pas afr						+					
Perlohmanniidae												
Perlohmannia dissimilis (Hewitt, 1908)	Per dis				+							
Phenopelopidae												
Eupelops occultus (Koch, 1835)	Eup occ	+			+							
Eupelops plicatus (Koch, 1836)	Eup pli	+	+									
Eupelops torulosus (Koch, 1840)	Eup tor		+									
Peloptulus gibbus Mihelčič, 1957	Pel gib	+			+							
Phthiracaridae												
*Phthiracarus*cf *anonymus* Grandjean, 1934	Pht ano		+									
Phtiracaruscompressus Jacot, 1930	Pht com							+				
*Phthiracarus*cf *laevigatus* Koch, 1844	Pht lae		+					+				
Steganacarus magnus (Nicolet, 1855)	Steg mag		+									
Atropacarus striculus (Koch, 1835)	Atr str	+	+					+				
Haplozetidae												
Protoribates capucinus Berlese, 1908	Protb ca	+		+								
Mycobatidae												
Minunthozetes semirufus (Koch, 1841)	Min sem	+		+	+			+	+	+		
*Punctoribates*nr *hexagonus* Berlese, 1908	Pun hex			+								
Punctoribates punctum (Koch, 1839)	Pun pun	+		+	+							
Zachvatkinibates perlongus (Balogh, 1959)	Zac per				+							
Quadroppiidae												
Quadroppia pseudocircumita Minguez et al., 1985	Qua pse		+									

Scheloribatidae									
Scheloribates laevigatus (Koch, 1835)	Sch lae		+		+				
Scutoverticidae									
Scutovertex sculptus Michael, 1879	Scuv scu		+				+		
Sphaerochthoniidae									
Sphaerochthonius splendidus (Berlese, 1904)	Sph spl		+						
Suctobelbidae									
Suctobelba sp.(Paoli, 1908)	Sucb sp		+						
*Suctobelbella*nr *arcana* Moritz, 1970	Suc arc		+					+	
Suctobelbella acutidens (Forsslund, 1941)	Suc acu	+	+						
Suctobelbella falcata (Forsslund, 1941)	Suc fal		+		+			+	
Suctobelbella lobata (Strenzke, 1951)	Suc lob		+						
*Suctobelbella*nr *latirostris* (Strenzke, 1950)	Suc lat		+						
*Suctobelbella*nr *tuberculata* (Strenzke, 1950)	Suc tub		+						
Suctobelbella sarekensis (Forsslund, 1941)	Suc sar		+						
Suctobelbella similis (Forsslund, 1941)	Suc sim		+	+				+	
Suctobelbella sp.Jacot, 1937	Suc sp		+		+			+	
Suctobelbella subtrigona (Oudemans, 1916)	Suc sub		+					+	
Tectocepheidae									
Tectocepheus velatus (Michael, 1880)	Tec vel	+	+	+	+	+		+	+
Thyrisomidae									
Banksinoma lanceolata (Michael, 1885)	Ban lan	+	+					+	
Pantelozetes paolii (Oudemans, 1913)	Pan pao	+			+				
Pantelozetes sp.(Grandjean, 1953)	Pan sp				+				
Zetomimidae									
Zetomimus furcatus (Pearce & Warburton, 1906)	Zet fur		+						
Zetorchestidae									
Zetorchestes falzonii (Coggi, 1898)	Zet fal		+						

Mesostigmata												
Ameroseiidae												
Ameroseius corbiculus (Sowerby, 1806)	Ame cor				+							
Ascidae												
Arctoseius sp.Sig Thor, 1930	Arcto sp				+							
Arctoseius cetratus (Sellnick, 1940)	Arc cet											
Asca aphidioides (Linné, 1758)	Asc aph					+			+			
Asca bicornis (Canestrini et Fanz., 1887)	Asc bic	+	+			+			+			
Cheiroseius borealis (Berelese, 1904)	Che bor											
Zercoseius spathuliger (Leonardi, 1899)	Zer spa					+			+			
Eviphididae												
Alliphis siculus (G. et R. Canestrini, 1881)	All sic				+				+	+		
Eviphis ostrinus (Koch, 1836)	Evi ost				+							
Hypoaspididae												
Geolaelaps aculeifer (Canestrini, 1883)	Geo acu	+	+			+						
Gymnolaelaps myrmecophilus (Berlese, 1892)	Gym myr	+										
Hypoaspis sp.(Canestrini, 1885)	Hypoas sp	+	+				+					
Macrochelidae												
Macrocheles penicilliger (Berlese, 1904)	Mac pen	+				+						
Pachylaelapidae												
Pachylaelaps squamifer Berlese, 1920	Pac squ					+						+
Pachylaelaps tesselatus Berlese, 1920	Pac tes				+							
Parasitidae												
Amblygamasus nr *hamatus* (C.L. Koch, 1839)	Amb ham	+										
Gamasodes sp.(Oudemans, 1939)	Gamaso sp				+							
Holoparasitus calcaratus (C. L. Koch, 1839)	Hol cal					+			+			
Leptogamasus sp.Trägardh, 1939	Lepto sp				+	+						
Lysigamasus misellus Berlese, 1904	Lys mis					+						
Lysigamasus nr *armatus* Halbert, 1915	Lys arm	+	+									

Lysigamasus parrrunciger Bhattachar., 1963	Lys par				+			
Lysigamasus runciger Berlese, 1904	Lys run		+	+				
Lysigamasus vagabundus Karg, 1968	Lys vag		+					
Paragamasus nr *diversus* (Halbert, 1915)	Parg div				+			
Paragamasus sp.Hull, 1918	Parg sp	+		+				+
Pergamasus barbarus Berlese, 1904	Perg bar			+				
Pergamasus crassipes (Linné, 1758)	Perg cra	+		+	+			
Phytoseiidae								
Amblyseiusmeridionalis Berlese, 1914	Amb mer		+		+			
Amblyseius obtusus (C.L. Koch, 1839)	Amb obt		+					
Amblyseius sp.Berlese, 1904	Ambl sp	+			+			
Podocinidae								
Lasioseiusberlesei (Oudemans, 1938)	Las ber				+			
Polyaspididae								
Polyaspinus cylindricus Berlese, 1916	Pol cyl				+			
Rhodacaridae								
Dendrolaelaps sp1	Denl apo	+						
Dendrolaelaps sp2	Denl rec			+				+
Dendrolaelaps stammeri Hirschmann, 1960	Den sta	+	+	+	+			+
Dendroseius reticulatus (Sheals, 1956)	Dens ret					+		
Rhodacarellus epyginialis Sheals, 1956	Rho epy		+					
Rhodacarellus silesiacus Willmann, 1935	Rho sil	+			+			
Rhodacaridae	Rhodac			+				+
Rhodocarus coronatus Berlese, 1921	Rho cor		+	+				+
Rhodocarusclavulatus Athias-Heiot, 1961	Rho cla	+						
Rhodocarus willmanii (Willmann, 1934)	Rho will	+	+					
Trachytidae								
Trachytes aegrota (C.L. Koch, 1841)	Tra aeg		+					+
Urodinychidae								

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Nanorchestes sp. Topsent et Trauessar, 1890	Nanorc sp					+		+	
Paratydeidae									
Paratydeidae Baker, 1949	Partydei					+	+		
Pseudocheylidae									
Pseudocheylidae Oudemans, 1909	Pseudoch						+		
Pyemotidae									
Pyemotes sp.Amerling, 1861	Pyemotes						+		
Pygmephoridae									
Bakerdania sp.Sasa, 1961	Bake sp	+	+	+				+	+
Rhagidiidae									
Poecilophysis sp. Cambridge, 1876	Poe sp	+	+						
Scutacaridae									
Scutacarus brevipes Mahunka, 1963	Scu brev			+	+			+	
Scutacarus crassisetus (Paoli, 1911)	Scu cra	+			+				
Scutacarus eucomus (Berlese, 1908)	Scu euc			+				+	
Scutacarus lapponicus (Willmann, 1943)	Scu lap			+				+	
Scutacarus major (Paoli, 1911)	Scu maj	+							
Scutacarus plumosus (Paoli, 1911)	Scu plu	+			+			+	
Scutacarus quadrangularis (Paoli, 1911)	Scu qua	+		+	+			+	
Scutacarus spinosus Storkán, 1936	Sci spi	+							
Tarsonemidae									
Steneotarsonemus sp.Beer, 1954	Sten sp							+	+
Tarsonemus sp.Can. et Fan., 1876	Tar sp	+		+	+				
Trombidiidae									
Speleorchestes sp.Trägårdh, 1909	Spel sp			+		+	+		
Tydeidae									
Microtydeus sp. Sig Thor, 1931	Mictydea					+	+		
Tydeidae P. Kramer, 1877	Tydeid		+			+	+		

Astigmata									
Astigmata (others)	Astig			+	+				+
Acaridae									
Schwiebea sp. Oudemans, 1916	Schw sp	+		+				+	
Tyrophagus sp.Oudemans, 1924	Tyro sp	+	+	+	+	+	+	+	+

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[i] Some species from this genus are considered to be a separate genus, *Zygoribatula*, in Weigmann (2006)